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Characteristics of the Grain-filling Process and Starch Accumulation of High-yield Common Buckwheat 'cv. Fengtian 1' and Tartary Buckwheat 'cv. Jingqiao 2'

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High-yield common buckwheat 'cv. Fengtian 1' (FT1) and tartary buckwheat 'cv. Jingqiao 2' (JQ2) were selected to investigate the characteristics of the grain-filling process and starch accumulation of high-yield buckwheat. FT1 had an average yield that was 43.0% higher than that of the control 'cv. Tongliaobendixiaoli' (TLBDXL) in two growing seasons, while JQ2 had an average yield that was 27.3% higher than that of the control 'cv. Chuanqiao 2' (CQ2). The Richards equation was utilized to evaluate the grain-filling process of buckwheat. Both FT1 and JQ2 showed higher values of initial growth power and final grain weight and longer linear increase phase, compared with respective control. These values suggest that the higher initial increasing rate and the longer active growth period during grain filling play important roles to increase buckwheat yield. Similar patterns of starch, amylose and amylopectin accumulation were detected in common buckwheat, leading to similar concentration of each constituent at maturity in FT1 and TLBDXL. Tartary buckwheat showed an increasing accumulation pattern of amylose in developing seeds, which differed from that of starch and amylopectin. This pattern led to a significant difference of the concentrations of amylose and amylopectin at maturity between JQ2 and CQ2, the mechanisms of which remained unclear. Nevertheless, both FT1 and JQ2 showed increased starch, amylose, and amylopectin accumulation during the physiological maturity of grains. The results suggest that prolonging the active grain-filling period to increase carbohydrate partitioning from source to seed sink can be an effective strategy to improve buckwheat yield.

Keywords: buckwheat, yield, Richards equation, starch, amylose

Introduction

Buckwheat (*Fagopyrum* Mill.) is usually classified as a cereal as it has several similarities to other cereals. However, buckwheat has some distinct characteristics compared with conventional cereals (Mazza 1988; Wijngaard and Arendt 2006). Buckwheat contains high amounts of polyphenolic compounds, such as flavonoids – specifically Rutin, which provides many health benefits to humans such as neuroprotection, anticancer, anti-inflam-

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matory, and the improvement of plasma cholesterol, hypertension and diabetes (Couch et al. 1946; Steadman et al. 2001a; Milde et al. 2004; Qin et al. 2010; Choi et al. 2015; Giménez-Bastida and Zieliński 2015). Therefore, buckwheat is recognized as an important raw material for functional food source in many countries, including China and Japan (Ötles and Cagindi, 2006; Bystrická et al. 2011; Chen, 2012; Ahmed et al. 2014).

Buckwheat is widely produced in many extreme environmental regions because of its ecological adaptability (Jacquemart et al. 2012). The cultispecies of *Fagopyrum* can be classified into two types: common buckwheat *(Fagopyrum esculentum)* and tartary buckwheat *(Fagopyrum tataricum).* Typically, common buckwheat is grown at lower altitudes, such as the northeast, northwest and northern parts of China, whereas tartary buckwheat is grown at higher altitudes, such as the southwest of China (Chen 2012). In the international market, the demand for buckwheat products is rapidly increasing; however, its low productivity hinders the development of the buckwheat industry (Jacquemart et al. 2012). Many strategies have been attempted in both common and tartary buckwheat breeding to improve its productivity. In the past few years, a number of buckwheat varieties have been developed in China (Ma et al. 2015).

Crop yield is mainly determined by the grain-filling stage. To date, many polynomial growth equations, such as logistic regression and Richards growth equation, have been utilized to evaluate the grain-filling process in many crops (Zhu et al. 1988; Li et al. 2006; Shi et al. 2013). Among these equations, the Richards equation has been suggested as the most suitable model to analyze crop growth (Li and Zeng 1985; Peng and Xiao 2012). However, to our knowledge, research about the buckwheat grain-filling process has yet to be reported.

Developing buckwheat seeds synthesize storage metabolites during grain filling. Starch is the major storage metabolite in the endosperm and accounts for approximately 75% of a seed's dry weight (Obendorf et al. 1993; Steadman et al. 2001a). Starch accumulation plays an important role in seed morphogenesis. The chemical components of buckwheat starch are similar to other types of crop starch that are mainly composed of amylose and amylopectin (Zheng et al. 1998). The starch pasting profiles of buckwheat have been reported to be different from the other crops, such as wheat; however, they are similar for both common and tartary buckwheat (Li et al. 1997). Meanwhile, some buckwheat varieties contain a higher amount of amylose accounting for approximately 50% of dry weight, compared with normal varieties with approximately 20% of amylose (Soral-Śmietana et al. 1984).

Guizhou Province is one of the centers of origin of buckwheat (Murai and Ohnishi 1996; Chen 1999; Tsuji and Ohnishi 2000). In a survey of yield performance of buckwheat varieties, high-yielding common buckwheat 'cv. Fengtian 1' and tartary buckwheat 'cv. Jingqiao 2' were identified based on their better growth and higher yield, compared with the other varieties. In this study, grain-filling characteristics and starch accumulation patterns of these two high-yield buckwheat varieties were investigated.

Materials and Methods

Plant materials and growth

High-yield common buckwheat ‘cv. Fengtian 1’ (FT1) and tartary buckwheat ‘cv. Jinqiao 2’ (JQ2) were studied. The common buckwheat ‘cv. Tongliaobendixiaoli’ (TLBDXL) and tartary buckwheat ‘cv. Chuanqiao 2’ (CQ2) were used as controls. The experiment was conducted at the Experiment Station of the Research Center of Buckwheat Industry Technology in Guizhou Province, China (908 m, 26°35′ N, 106°52′ E) during the two growing seasons in 2012 and 2013. The soil was yellow loam that contained 17.6 $g \cdot kg^{-1}$ organic matter, 1.06 $g \cdot kg^{-1}$ total nitrogen, 111 $mg \cdot kg^{-1}$ alkaline nitrogen, 8.0 $mg \cdot kg^{-1}$ valid phosphorus, and 121 $mg \cdot kg^{-1}$ valid potassium, which was tested in 2013. The experimental set up was a randomized block design with three replications. Buckwheat seeds were sown in middle October in 2012 and late March in 2013. The area for each test plot was 2 m × 10 m, which the spacing for each row was 40 cm. Before sowing, 30 kg N ha^{-1}, 60 kg P_2O_5 ha^{-1}, and 30 kg K_2O ha^{-1} were applied as base fertilizer. Normal agricultural practice was implemented during the two growing seasons. In 2013, about 1000 to 1200 plants for each plot with uniform growth were selected and tagged before flowering. About 10 to 15 tagged plants from each plot were sampled every 7 d from 10 d after flowering (7 d after heading) to maturation in order to determine the grain-filling process and metabolites.

Sample preparation and grain constituent analysis

The samples were dried at 70 °C for 72 h to constant weight. Starch concentration was determined by a spectrophotometric method (He and Zhang 1997). Approximately 40 mg sample was mixed with 1 mL of 95% ethanol for three times to remove the soluble sugars. Approximately 10 mL of distilled water was added to the residue and the slurry was boiled for 10 min. The solution was alkalized by adding 5 mL of 0.5 mol/L NaOH and diluted with distilled water to 50 mL, of which 2 mL was reacted with anthrone reagent (containing 1% of anthrone and 72% of H_2SO_4) by boiling for 10 min. After cooling the solution to room temperature, the absorbance was read at 620 nm. Starch concentration was calculated using a glucose standard solution curve. The amount of starch in each grain was calculated using grain weight and multiplying it with starch concentration to assess starch accumulation pattern. The concentrations of amylose and amylopectin were determined according to the method proposed by Wang (1999). A sample of approximately 100 mg was eluted by 2 mL of 95% ethanol for three times to remove soluble sugars. Then, 9 mL of 1 mol/L NaOH was added to the residual to boil for another 10 min. The solution was diluted with distilled water to 100 mL, of which 5 mL was diluted with 50 mL distilled water and then acidified by 1.0 mL of 1 mol/L acetic acid. The mixed liquor was stained by 2 mL I_2/KI solution (containing 0.2% I_2 and 2% KI) and diluted with distilled water to 100 mL. After 10 min, the absorbance was read at 620 nm and 460 nm. Amylose concentration was calculated using a potato starch standard curve. Amylopectin concentration was calculated using starch concentration subtracting amylose concentration. To assess the amylose and amylopectin accumulation patterns, their respective amounts in each grain were calculated using grain weight and multiplying it with amylose and amylopectin concentration, respectively. Plant height, the number of stem branches, the number of stem nodes, the grain number per plant, the grain weight per plant and the thousand-seed weight were determined from ten plants that were randomly sampled from each plot at maturity. The yield of each plot was determined at maturity

The Richards equation was used to determine the grain-filling process. The days after flowering (t) was set as the independent variable, and the seed weight (W) was set as the dependent variable as follows:

$$W = A/(1 + B^{-Kt})^{1/N}.$$

W represents the grain weight of buckwheat during grain filling, A represents the final grain weight at harvest, B represents the initial value of parameter, K represents the constant growth rate, N represents the shape parameter, t represents the time after flowering (the flowering day was marked as 0 d), and R^2 represents the compatibility.

$$G = (KW/N)\,[1 - (W/A)^N]\,,$$

$$R = (K/N)\,[1 - (W/A)^N]\,,$$

$$R_0 = K/N$$

G represents the growth in unit time during grain filling, R represents the relative growth rate, and R_0 represents the initial growth power.

$$T_{\max.G} = (\ln B - \ln N)/K$$

$$W_{\max.G} = A(N + 1) - 1/\mathrm{N}$$

$$V_{\max} = (KW_{\max\cdot G}/N)\,[1 - (W_{\max.G}/A)\mathrm{N}]$$

$$t_1 = -\ln\left[N^2+3N+N\sqrt{N^2+6N+5)}\,/\,2B\right]\Big/K$$

$$t_2 = -\ln\left[N^2+3N+N\sqrt{N^2+6N+5)}\,/\,2B\right]\Big/K$$

$T_{\max.G}$ represents the time with maximum grain-filling rate, $W_{\max.G}$ represents the growth at the day with maximum grain-filling rate, $V_{\max}$ represents the maximum grain-filling rate, t_1 represents the starting day of the maximum grain-filling period, and t_2 represents the ending day of the maximum grain-filling period.

Statistical analysis

All data were classified using MS-Excel. The means and differences of the data from three replications were determined by SPSS 17.0 (SPSS Inc., Chicago, IL, USA). Error bars represent standard deviation.

Results

Agronomic traits

The high-yield common buckwheat FT1 and tartary buckwheat JQ2 were compared with the lower yield variety TLBDXL and CQ2, respectively, for the major agronomic traits and yield (Table 1). The plant height of the tested varieties exhibited wide environmental variations in two growing seasons. FT1 showed higher plant height than TLBDXL, whereas JQ2 showed lower plant height than CQ2, regardless of growing seasons. Although the stem branch number of FT1 was lower than TLBDXL, FT1 produced more grains per plant. JQ2 showed a higher stem branch number, stem node number, and grain number per plant than those of CQ2 in both growing seasons. At maturity, FT1 had an average yield that was 43.0% higher than that of TLBDXL, whereas JQ2 had an average yield that was 27.3% higher than that of CQ2 in two growing seasons. During spring 2013, all tested varieties showed better growth and higher yield. FT1 and JQ2 harvested 1.7 and 2.7 t ha^{-1}, respectively, which increased by 46.6% and 41.0%, compared to respective control.

Table 1. The major agronomic traits of buckwheat determined in two growing seasons

Year	Variety	Plant height (cm)	Stem branch number per plant	Stem node number per plant	Grain number per plant	Yield (kg/hm^2)
2012	FT1	87.0c	3.4c	9.0b	116.4a	1519.2b
	TLBDXL	75.2c	4.2b	8.8b	103.2b	1091.0c
2013	FT1	109.0a	4.2b	10.8a	94.0bc	1729.5a
	TLBDXL	95.4b	5.2a	11.1a	87.3c	1179.4c
2012	JQ2	129.4b	7.6a	15.6ab	519.0a	1845.1b
	CQ2	93.8d	5.0c	13.8c	491.0a	1623.2c
2013	JQ2	147.9a	6.8b	16.6a	220.2b	2732.9a
	CQ2	118.5c	6.6b	14.7b	204.7b	1938.4b

Values represent the mean of three replicates. Different small letters indicate the significant difference ($P \leq 0.05$) among the same cultispecies analyzed by LSD using SPSS 17.0.

Simulation of grain-filling process

The buckwheat grain-filling process from 7 d to 21 d after heading to maturity during spring 2013, FT1 showed similar pattern of grain development to TLBDXL (Fig. 1). FT1 then accumulated more dry materials in grains from 21 d after heading to maturity. JQ2

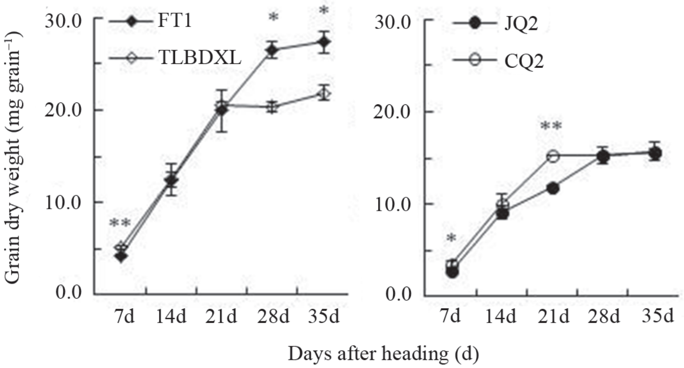

Figure 1. Changes of the grain dry weight during grain filling. Values represent the mean of three replicates± standard deviation. Differences between the high-yield buckwheat and low-yield buckwheat were analyzed by Student's *t*-test. Significant differences are indicated by asterisks ($*P\leq0.05$; $**P\leq0.01$)

exhibited a slower grain-filling rate compared to CQ2 21 d after heading. However, it achieved a similar grain dry weight at maturity. In addition, both common buckwheat varieties showed higher grain weight than the tartary buckwheat varieties.

In the Richards equation the R^2 value for curve equations ranged from 0.994–0.999 (Table 2). This finding indicates that the Richards equation can be used to evaluate the grain-filling process of buckwheat. Both FT1 and JQ2 showed lower values of B, K, N and $T_{\max.G}$, but had higher values of A and R^0, compared with respective control. FT1 also showed a lower $V_{\max}$ value than TLBDXL, however, JQ2 showed a higher $V_{\max}$ value than CQ2. In addition, both FT1 and JQ2 showed a shorter lag phase and longer linear increase phase, compared to respective control (Fig. 2). However, only FT1 accumulated a significant higher 1000-grain weight than TLBDXL at maturity. JQ2 showed a similar value of 1000-grain weight to CQ2 (Table 2).

Starch accumulation

FT1 showed a fast accumulation pattern of starch, amylose and amylopectin until 28 d after heading (Fig. 3). TLBDXL mainly accumulated those grain constituents before 21 d after heading, leading to a significant difference of storage starch contents between the

Table 2. The parameters of the Richards equation for evaluating grain-filling process of buckwheat

Variety	A (g·100-grain^{-1})	B	K	N	R^2	R_0	$T_{\max.G}$ (mg grain^{-1}·d^{-1})	$V_{\max}$ (mg·grain^{-1}·d^{-1})
FQ1	2.95	1.14	0.13	0.15	0.999	0.86	16.44	1.26
TLBDXL	2.19	1380.60	0.37	2.26	0.997	0.17	17.15	1.49
JQ2	1.62	1.53	0.15	0.19	0.998	0.77	14.50	1.22
CQ2	1.55	2324.61	0.43	2.21	0.997	0.19	16.27	0.79

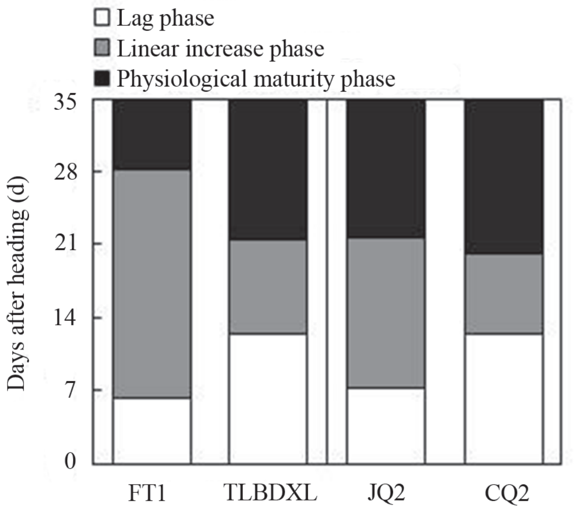

Figure 2. The division of the typical grain-filling stage of buckwheat

two common varieties at maturity. Similarly, JQ2 showed a longer accumulation period of starch and amylopectin, However, CQ2 exhibited a rapid accumulation pattern of starch and amylopectin, leading to similar amounts of starch between the two tartary buckwheat varieties at maturity. Compared with common buckwheat, tartary buckwheat showed an increased accumulation pattern of amylose during grain filling. In addition, the amount of amylose in JQ2 was lower than that of CQ2 during grain filling.

At maturity, no significant differences among starch, amylose, and amylopectin concentration were found between FT1 and TLBDXL (Table 3). Although JQ2 showed similar starch concentration to CQ2, the concentrations of amylose and amylopectin of JQ2 were significantly different, thus exhibiting a lower amylose concentration but a higher amylopectin concentration in JQ2 (Table 3).

Table 3. The 1000-grain weight and the concentrations of starch, amylose and amylopectin of buckwheat at maturity during spring 2013

Variety	1000-grain weight (g)	Starch (%)	Amylose (%)	Amylopectin (%)
FT1	27.40a	79.65a	20.06a	59.58a
TLBDXL	21.82b	79.40a	20.21a	59.19a
JQ2	15.69a	78.79a	22.26b	56.54a
CQ2	15.65a	78.77a	27.23a	51.54b

Values represent the mean of three replicates. Different small letters indicate the significant difference ($P \leq 0.05$) among the same cultispecies analyzed by Student's *t*-test using SPSS 17.0.

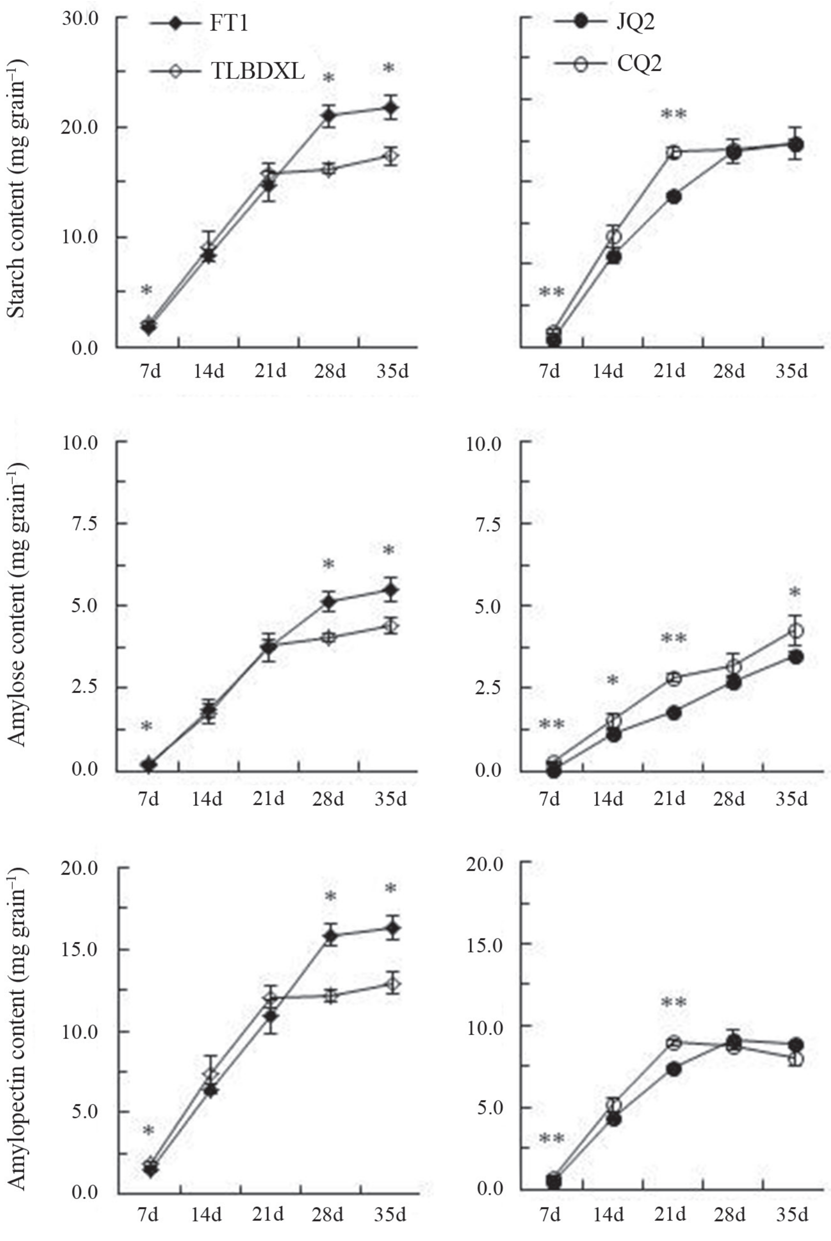

Figure 3. Changes of the amounts of starch, amylose and amylopectin in each grain during grain filling. Values represent the mean of three replicates ± standard deviation. Differences between the high-yield buckwheat and low-yield buckwheat were analyzed by Student's *t*-test. Significant differences are indicated by asterisks (*$P \leq 0.05$; **$P \leq 0.01$)

Discussion

Buckwheat has a low and erratic seed yield characteristic, which caused a progressive decrease of cultivated area over the last 20 to 30 years (Jacquemart et al. 2012). The average buckwheat yield differs in varieties and countries. In some countries, buckwheat produced the highest yield of up to 3.4 t ha^{-1} in 2010; however, in China the yield was 0.8 t ha^{-1} (FAOSTAT, 2012). Recently, buckwheat high-yield breeding work has been proposed in China and many varieties have been established (Ma et al. 2015). We previously identified common buckwheat FT1 and tartary buckwheat JQ2 as high-yield varieties grown in Guizhou Province. FT1 and JQ2 produced significantly higher yields during the spring and fall growing seasons, compared with respective control (Table 1). FT1 averaged 43.0% higher yield than TLBDXL during the two growth seasons. During spring 2013, FT1 and JQ2 harvested 1.7 t and 2.7 t ha^{-1}, which increased by 46.6% and 41.0%, respectively, compared with respective control. These results indicate that the buckwheat high-yield breeding work in China has achieved an important target.

In this study, we utilized the Richards equation to characterize the grain-filling process of buckwheat. Both common and tartary buckwheat showed a high value of R^2 (0.994–0.999), indicating that the equation can be used to describe the grain-filling process of buckwheat. The high-yielding variety FT1 showed higher values of A and R^0 and longer linear increase phase, compared with TLBDXL, indicating that the higher initial increase rate and longer active growth period during grain filling play important role to improve grain weight of FT1. The high-yield variety JQ2 showed higher values of A, R^0, $V_{\max}$, and linear increase phase but exhibited a lower value of $T_{\max.G}$, leading to the similar grain weight to CQ2. The length of growth period is an important factor affecting buckwheat yield (Li et al. 2013). Buckwheat is well known as a relief crop because of its shorter growth period, compared with other crops. However, the short growth period leads to reduced photosynthates which adversely limits carbohydrate partitioning and starch accumulation of buckwheat. Both high-yield buckwheat varieties showed a longer linear increase phase at the reproductive stage. This finding suggests that prolonging the active grain-filling period is an effective strategy to increase buckwheat yield.

Starch accounts for approximately 75% of dry buckwheat seed weight (Obendorf et al. 1993; Steadman et al. 2001b). The accumulation pattern of starch was closely related to grain weight during grain filling (Figs 1 and 3). The amylose and amylopectin accumulation patterns of common buckwheat were closely related to those of starch and grain weight during grain filling. However, tartary buckwheat showed increased accumulation pattern of amylose that differed from that of starch and amylopectin during grain filling. Nevertheless, both FT1 and JQ2 showed increasing accumulation patterns of starch, amylose, and amylopectin during physiological maturity phase, suggesting that the carbohydrate partitioning and remobilization can be manipulated to improve buckwheat yield.

Both FT1 and JQ2 showed significantly higher yields than respective control due to higher initial increased rate and prolonged active growth period during grain filling. Given the increasing accumulation patterns of starch, amylose, and amylopectin during physiological maturity phase in FT1 and JQ2, we suggest that prolonging the active grain-filling period to enhance carbohydrate partitioning from source to seed sink might be an effective strategy for improving buckwheat yield.

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